

Monophyly, Interrelationships and Description of Three New Genera in the Dottyback Fish Subfamily Pseudoplesiopinae (Teleostei: Perciformes: Pseudochromidae)

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ABSTRACT. Within the Pseudochromidae, the subfamily Pseudoplesiopinae is diagnosed by six unequivocal autapomorphies: single tubed lateral-line scale; posterior part of pelvic bone with triangular or hook-shaped lateral process; base of anterior process on pelvic bone posteriorly positioned; coracoid articulates ventrally with medial face of lateral lamina of cleithrum; basihyal bound to anterior face of basibranchial 1; and urohyal with prominent dorsally directed process. Five genera are recognised in the subfamily. *Pseudoplesiops* Bleeker (*Nematochromis* Weber is a junior synonym), with seven nominal species, is diagnosed by a single autapomorphy: medial laminae of pelvic bones expanded dorsally. *Chlidichthys* Smith (*Wamizichthys* Smith is a junior synonym), with 10 nominal species, is diagnosed by two autapomorphies: lower lip incomplete; and second infraorbital bone absent. *Pectinochromis* n.gen. (type species *Pseudoplesiops lubbocki* Edwards & Randall), with a single nominal species, is diagnosed by five autapomorphies: second dorsal-fin pterygiophore inserting between neural spine 3 and 4; second supraneural bone absent; first dorsal-fin pterygiophore expanded anteriorly; first dorsal-fin pterygiophore with lateral processes; and gill rakers relatively numerous. *Amsichthys* n.gen. (type species *Pseudoplesiops knighti* Allen), with a single nominal species, is diagnosed by a single autapomorphy: upper preopercular pore usually absent. *Lubbockichthys* n.gen. (type species *Pseudoplesiops multisquamatus* Allen), with a single nominal species, is diagnosed by four autapomorphies: scales small; scales cycloid at all stages of ontogeny; some head bones with weakly honeycombed surface; and parietal enclosing dorsal part of supratemporal laterosensory canal. A parsimony analysis of various characters of the laterosensory system, caudal skeleton, dorsal-fin osteology, and fin-ray branching supports the following relationships: (*Lubbockichthys* ((*Amsichthys* + *Pseudoplesiops*) (*Chlidichthys* + *Pectinochromis*))).

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The Pseudochromidae is a family of small, reef-associated fishes, which are distributed throughout the Indo-Pacific. The family is currently divided into four subfamilies: Anisochrominae, Congrogadinae, Pseudochrominae and Pseudoplesiopsinae (Godkin & Winterbottom, 1985). The objectives of the present paper are to provide evidence for monophyly of the Pseudoplesiopsinae, to diagnose its included genera, and to investigate phylogenetic relationships among those genera. Species-level revisions of the genera will be provided in forthcoming papers by the present authors.

Historical review of the systematics of the Pseudoplesiopsinae

Bleeker (1858) described the genus *Pseudoplesiops* for a new species, *P. typus*, from a single specimen from Goram (= Manawoka), Indonesia. He assigned it to his family Pseudochromides [sic], noting that it fell between *Pseudochromis* Rüppell and *Plesiops* Oken (now Plesiopidae) in morphology. He described it as having: dorsal fin with 16 unbranched and nine or 10 branched rays; anal fin with seven unbranched and nine branched rays; pelvic fin with no spine and five rays, the outer two elongate and filiform; palatine teeth absent; scales cycloid; and a single anterodorsal lateral line consisting of inconspicuously pored scales. He later (Bleeker, 1875) reported on an additional specimen of the species from Ambon (actually referable to a new *Pseudoplesiops* species, which we will describe elsewhere) and included the species as sole member of the Pseudoplesiopsini, one of three groupings he recognised within his family "Pseudochromidoïdes." The remaining two groupings were Cichlopini, for *Cichlops* Müller & Troschel (= *Labracinus* Schlegel), *Pseudochromis* Rüppell, *Pseudogramma* Bleeker (now in Serranidae), *Gramma* Poey (now in Grammatidae) and *Trachinops* Günther (now in Plesiopidae), and Plesiopini for *Plesiops* Oken and *Paraplesiops* Bleeker (both now in Plesiopidae).

Günther (1860) assigned *Pseudoplesiops* to his Pseudochromides, which he treated as a subgroup of the Trachinidae, along with *Pseudochromis*, *Cichlops*, *Opisthognathus* [sic] Cuvier (now Opisthognathidae), *Notothenia* Richardson (now Nototheniidae), *Harpagifer* Richardson (now Harpagiferidae), *Heterostichus* Girard (now Clinidae) and *Pegetodes* Richardson (now Channichthyidae).

Boulenger (1895: 336) listed *Pseudoplesiops* in the Serranidae and noted that it "appears to combine characters of *Callanthias* [now in Callanthiidae] and *Plesiops*." Boulenger did not comment on the position of *Pseudochromis* and *Cichlops* in this paper, but later (Boulenger, 1901) placed them and genera now assigned to the Opisthognathidae, Malacanthidae and Bathymasteridae in the Pseudochromidae.

Boulenger (1899) apparently overlooked Bleeker's (1858) use of *Pseudoplesiops* (despite his own 1895 reference to *Pseudoplesiops* Bleeker) and described *Pseudoplesiops* as a new genus for a new species of cichlid from the Congo, *P. nudiceps*. He later (1902) described

another new species in the genus from the Congo, *P. squamiceps*. Pellegrin (1904) noted that *Pseudoplesiops* Boulenger was preoccupied and proposed a replacement name, *Nanochromis* (often subsequently misspelt *Nannochromis*).

Regan (1913) classified *Pseudoplesiops* in its own family, Pseudoplesiopidae, but included *Pseudochromis* and *Cichlops* in the Serranidae.

Weber (1913) described a new genus and species, *Nematochromis annae*, from two syntypes collected in Indonesia during the Siboga Expedition, one from Sarasa Island, Postilon Islands, and the other from Solor Strait. He described the species as having: dorsal and anal fins with two weak spines and mostly undivided, segmented rays, totalling 26–27 and 15 rays, respectively; pelvic fin with a weak spine and three unbranched, segmented rays; and lateral line interrupted, consisting of an anterodorsal series of 30 grooved scales and a midlateral posterior series of 15 grooved scales. He assigned the species to the Pseudochromidae.

Jordan (1923) provided a classification for nominal fish genera. He included only *Pseudoplesiops* in the Pseudoplesiopidae, retaining *Nematochromis* in the Pseudochromidae.

Weber & de Beaufort (1929) reexamined the holotype of *Pseudoplesiops typus* and modified some of the characters given by Bleeker (1858). Most notably, they reported in the generic diagnosis that the pelvic fin had 1,4 rays, the first segmented ray thickened, produced and bifid, but reported in the species diagnosis that all segmented rays are simple, and that the anterior two are thickened and elongate. Weber & de Beaufort (1929, 1931) generally followed Regan's (1913) classification, but recognised the Pseudochromidae [sic] as a serranid subfamily containing *Nematochromis*, *Dampiera* Castelnau (= *Labracinus*), *Pseudochromis* and *Pseudogramma*.

Berg (1940) also followed Regan's assignment of *Pseudoplesiops* to its own family, while retaining "pseudochromids" in the Serranidae.

Fowler (1931) recognised three subfamilies within the Pseudochrominae: Pseudogramminae (*Pseudogramma*); Pseudochrominae (*Dampiera*, *Pseudochromis* and *Nematochromis*); and Pseudoplesiopsinae [sic] (*Pseudoplesiops*). He later (Fowler, 1934) described two new monotypic pseudoplesiopsine genera, *Loxopseudochromis* and *Opsipseudochromis*, from the Philippines.

Schultz (1943) described a new species, *Pseudoplesiops rosae*, from Rose Island, Phoenix Islands. He compared it with *P. typus* and assigned *Pseudoplesiops* to the Pseudochromidae, along with *Pseudochromis*, *Plesiops*, *Aporops* Schultz (now Serranidae) and *Pseudogramma*. He later (Schultz, 1953) synonymised *Nematochromis* with *Pseudoplesiops* and described an additional two species in the genus, *P. revellei* and *P. sargenti*. He also included acanthoclinids (now assigned to the Plesiopidae; see Mooi, 1993) in the Pseudochromidae.

Smith (1953) briefly described a new genus and species, *Chlidichthys johnvoelckeri* from east Africa. In the following year he reviewed pseudoplesiopsine [sic] fishes from south and east Africa (Smith, 1954). He ignored his

previous description and described *C. johnvoelckeri* again as a new genus and species, along with another new congener, *C. pembae*, and a second new genus and species, *Wamizichthys bibulus*. He also assigned *P. rosae* to *Chlidichthys*, and, in comparing *C. pembae* with similar species, noted that: "It will not be surprising if a careful examination of *Pseudoplesiops typus* Bleeker, and of *Nematochromis annae* Weber, prove them to be one and the same and identical with the above." He excluded Fowler's (1934) *Loxopseudochromis* and *Opsipseudochromis* to the Owstoniidae (now considered a synonym of the Cepolidae; see Gill & Mooi, 1993: 331).

Smith (1954) separated the Pseudoplesiopsinae from the Pseudochrominae, the only other pseudochromid subfamily he recognised, on the basis of the following characters: dorsal- and anal-fin spines weak and flexible (versus strong); most segmented rays in dorsal and anal fins simple (versus mostly or all branched); pelvic fins with a weak spine and three or four simple, segmented rays (versus with a spine and five branched, segmented rays); lateral line reduced to a tubed scale at the shoulder and at most a series of pitted scales along middle of side and peduncle (versus represented by an anterodorsal and a posterolateral series of tubed scales); dorsal and anal fins without basal scaly sheaths (versus with basal scaly sheaths); lower pectoral-fin proximal radial abutting against both coracoid and scapula (versus coracoid only); and vertebrae 11 + 16 (versus 10 + 16).

Böhlke (1960) recognised three separate families, Pseudochromidae, Anisochromidae and Pseudoplesiopidae, and included *Chlidichthys*, *Nematochromis*, *Pseudoplesiops* and *Wamizichthys* in the latter.

Norman (1966) included *P. typus* as sole member of the Pseudoplesiopinae, which he regarded as a subfamily of the Plesiopidae. He recognised the Pseudochrominae as a subfamily of the Serranidae, in which he placed *Nematochromis* [as well as *Pseudochromis*, *Dampiera*, *Nesiotes* De Vis (= *Cypho* Myers), *Pseudochromichthys* (= *Plesiops*, Plesiopidae; see Mooi, 1996), *Pseudocrenilabrus* Fowler (now in Cichlidae), *Pseudogramma* and *Gramma*].

Lubbock reviewed pseudochromids of the Red Sea and northwestern Indian Ocean (Lubbock, 1975), central Indian Ocean (Lubbock, 1976) and western Indian Ocean (Lubbock, 1977). He recognised a total of nine pseudoplesiopine species in these papers, six of which he described as new. He placed all of the species in *Chlidichthys*, including the monotypic *Wamizichthys*.

Springer *et al.* (1977) synonymised the Anisochromidae with the Pseudochromidae, and proposed that the Anisochromidae and Pseudoplesiopinae were more closely related to each other than either was to the Pseudochrominae. Springer *et al.* noted that several of Smith's (1954) pseudoplesiopine characters were shared with anisochromines, and were thus synapomorphies of the two subfamilies (fin spine development; reduction in number of pelvic-fin rays; presence of at least one unbranched pelvic-fin ray; absence of scale sheaths on dorsal and anal fins; and absence of tubed scales in posterolateral lateral

line). They diagnosed the Pseudoplesiopinae by the following autapomorphies: all segmented pelvic-fin rays simple; segmented dorsal-fin rays mostly simple; single tubed lateral-line scale; ventralmost proximal radial of pectoral fin articulates with coracoid and scapula; and all or almost all medial radials of dorsal- and anal-fin pterygiophores fused to proximal radials.

Edwards & Randall (1983) placed *Chlidichthys* in junior synonymy with *Pseudoplesiops*, and described a distinctive new species from the Red Sea, *Pseudoplesiops lubbocki*.

Godkin & Winterbottom (1985) provided evidence for classification of the Congrogadidae, previously placed in the Blennioidei or Trachinoidei, as a subfamily of the Pseudochromidae, and the sister-group of the Anisochrominae; they proposed that the Pseudoplesiopinae is the sister-group of the Anisochrominae + Congrogadinae. In so doing, they noted that all of the synapomorphies proposed by Springer *et al.* (1977) to unite the Anisochrominae with the Pseudoplesiopinae were also found in the Congrogadinae. They also noted that one of the characters used by Springer *et al.* to diagnose the Pseudoplesiopinae was also found in the Congrogadinae (all or almost all medial radials of dorsal- and anal-fin pterygiophores fused to proximal radials), and that another was not found universally among pseudoplesiopines (ventralmost proximal radial of pectoral fin articulates with coracoid and scapula). They therefore concluded that only three of the pseudoplesiopine autapomorphies proposed by Springer *et al.* (1977) were valid: segmented pelvic-fin rays all simple; most segmented dorsal-fin rays simple; and a single tubed lateral-line scale. However, they overlooked that *Pseudoplesiops lubbocki* Edwards & Randall (1983) has mostly branched dorsal-fin rays.

Allen (1987) described three new species in the genus *Pseudoplesiops*: *P. multisquamatus*, *P. knighti*, *P. howensis*. He noted, however, that they exhibited characters that had been traditionally used to separate *Chlidichthys* from *Pseudoplesiops*. He therefore regarded the generic assignment of the three species provisional.

Gill *et al.* (1991) followed Schultz (1953) in placing *Nematochromis* in synonymy with *Pseudoplesiops*. They noted that the syntypes of *N. annae* represent two different, and otherwise undescribed, species. They therefore designated a lectotype for *N. annae*, and described the second species, *P. collare*, based on the paralectotype and an additional specimen (holotype) from Flores. They also noted that Schultz's *P. sargenti* is a junior synonym of *P. typus*.

Gill & Randall (1994) demonstrated monophyly for *Chlidichthys* (including all of the Red Sea and western and central Indian Ocean species recognised in Lubbock's papers) from synapomorphies associated with lower-lip and cephalic-laterosensory morphology, and described a new species from southern Oman, *C. cacatuoides*. They noted that *Pseudoplesiops lubbocki* was not referable to *Pseudoplesiops*, and that instead it shared some characters with *Chlidichthys*. They suggested that it should be placed in its own genus.

Materials and methods

Phylogenetic analyses were performed using the implicit enumeration option of Hennig86 version 1.5 (Farris, 1988). Character polarity was determined by outgroup comparison. The Anisochrominae + Congrogadinae were used as first outgroup following the scheme of relationships proposed by Godkin & Winterbottom (1985). *Assiculoides desmonotus* Gill & Hutchins and *Assiculus punctatus* Richardson were used as the second and third outgroups, respectively. Although both of these genera are currently classified in the Pseudochrominae, current evidence indicates that they form successive sister groups to a clade consisting of the Anisochrominae + Congrogadinae + Pseudoplesiopinae (Gill & Hutchins, 1997: 45).

Nomenclature of head pores follows Winterbottom (1986). When referring to fin rays, the term ray is used in its general sense to include both spinous (azygous, unsegmented, bilaterally fused) and soft rays.

Numerous pseudoplesiopine specimens and radiographs were examined for external (including superficial osteology) and post-cranial axial skeleton characters, respectively. These materials, which represented all known species, will be listed in our forthcoming generic revisions. Similarly, a more extensive listing of pseudochromine and non-pseudochromid specimens will be listed in a forthcoming paper on pseudochromid phylogeny and biogeography by the first author. The following cleared and stained pseudoplesiopine specimens (variously prepared following the methods of Taylor, 1967, Dingerkus & Uhler, 1977, and Potthoff, 1984) were examined (institutional codes follow Leviton *et al.*, 1985): *Amsichthys knighti*, AMS I.22612-034 (1: 28.3 mm SL), AMS I.21540-046 (3: 19.5–30.4 mm SL), ASIZ uncat. (2: 24.0–27.4 mm SL), USNM 306590 (1: 29.2 mm SL); *Chlidichthys* sp. 1, ROM uncat. (RW 88–15) (2: 33.5–38.1 mm SL); *C. auratus*, USNM 211780 (2: 37.5–37.8 mm SL); *C. bibulus*, BPBM 27310 (1: 26.8 mm SL); *C. cacatuoides*, BMNH 1994.4.19.1 (1 paratype: 37.2 mm SL); *C. inornatus*, AMS I.23653-002 (1: 27.9 mm SL), ROM CS857 (3: 30.0–37.0 mm SL); *C. johnvoelckeri*, CAS 35451 (2: 24.7–37.9 mm SL), ROM uncat. (RW 88–26) (2: 36.2–38.7 mm SL); *C. pembrae*, ROM uncat. (RW 88–15) (2: 21.2–23.3 mm SL); *C. rubiceps*, USNM 211777 (5: 12.0–15.0 mm SL), BMNH 1999.1.14.18 (1: 27.2 mm SL); *Lubbockichthys* sp. 1, AMS I.25107-067 (1: 47.3 mm SL); *L.* sp. 2, AMS I.39406-001 (1: 44.6 mm SL); *L.* sp. 3, AMS I.39407-001 (1: 37.2 mm SL); *L. multisquamatus*, AMS I.20779-175 (1: 36.3 mm SL); *Pectinochromis lubbocki*, BPBM 28119 (1 paratype: 35.5 mm SL); *Pseudoplesiops* sp. 1, AMS I.20756-014 (1: 25.7 mm SL); *P.* sp. 2, BMNH 1999.1.14.17 (1: 22.6 mm SL); *P. annae*, AMS I.21918-017 (1: 21.0 mm SL), USNM 270268 (2: 24.2–29.3 mm SL); *P. howensis*, AMS I.19755-024 (1: 21.0 mm SL); *P. rosae*, AMS I.22582-034 (3: 17.2–22.0 mm SL), BMNH 1999.1.14.14-16 (3: 18.0–21.4 mm SL); *P. typus*, AMS I.19442-013 (1: 50.6 mm SL), ROM CS585 (1: 49.0 mm SL). Our discussions of the morphology of immediate outgroups are largely based on details provided by Springer *et al.* (1977), Godkin & Winterbottom (1985) and Winterbottom (1986, 1996), and on the following cleared and stained specimens: ANISOCHROMINAE: *Anisochromis*

kenyae, RUSI 4906 (1: 23.3 mm SL); *A. straussi*, USNM 215859 (4 paratypes: 19.0–24.0 mm SL), USNM 257761 (1: 8.0 mm SL). CONGROGADINAE: *Blennodesmus scapularis*, AMS I.26723-087 (2: 49.7–54.1 mm SL), BMNH uncat. (1: 29.6 mm SL); *Congrogadus spinifer*, BMNH 1911.1.4.3-4 (1: c. 122 mm SL); *Congrogadus subducens*, AMS I.26723-051 (1: 49.3 mm SL), AMS I.26723-052 (1: 18.7 mm SL), AMS I.26723-057 (1: 135.0 mm SL), BMNH 1847.7.21.67-69 (1: c. 147 mm SL); *Halidesmus scapularis*, BMNH 1933.10.31.1-4 (1: c. 114 mm SL); *Haliophis guttatus*, BMNH 1951.1.16.606-608 (1: c. 82 mm SL). PSEUDOCHROMINAE: *Assiculoides desmonotus*, WAM P.30929-008 (2 paratypes: 41.3–46.2 mm SL); *Assiculus punctatus*, AMS I.13113 (1: 63.0 mm SL), NTM S.10016-009 (4: 21.7–51.9 mm SL).

Subfamily Pseudoplesiopinae

Pseudoplesiopini Bleeker, 1875: 4.

Diagnosis. Members of the subfamily are diagnosed by the following synapomorphies: single tubed lateral-line scale (character 1); posterior part of pelvic bone with triangular or hook-shaped lateral process for attachment of slip of hypaxial musculature (character 2); base of anterior process on pelvic bone posteriorly positioned (character 3); coracoid articulates ventrally with medial face of lateral lamina of cleithrum (character 4); basihyal bound to anterior face of basibranchial 1 (character 5); urohyal with prominent dorsally directed process (character 6). Two additional characters provide equivocal support for monophyly of the subfamily: dorsal profile of anterior ceratohyal straight, without excavation (remnant of beryciform foramen, *sensu* McAllister, 1968); and all medial radials of dorsal- and anal-fin pterygiophores fused to proximal radials. Both characters also occur in the Congrogadinae, but not in the Anisochrominae, their sister group. Therefore, they may be independent autapomorphies of the Congrogadinae and Pseudoplesiopinae, or they may be synapomorphies of the more inclusive Anisochrominae + Congrogadinae + Pseudoplesiopinae clade that have undergone “reversal” in the Anisochrominae. These two characters will be discussed in greater detail in a forthcoming paper on pseudochromid intrarelationships and biogeography by the first author.

Diagnoses of pseudoplesiopine genera

Lubbockichthys n.gen.

Figs. 1, 9A, 10A, 12A, 13A, 14A

Type species. *Pseudoplesiops multisquamatus* Allen, 1987.

Diagnosis. *Lubbockichthys* is distinguished from other pseudoplesiopines by the following four autapomorphies: parietal enclosing dorsal part of supratemporal laterosensory canal (character 7); also occurs homoplastically in *Pseudoplesiops howensis*; scales cycloid at all stages of ontogeny (character 8); scales small, scales in lateral series 51–66 (character 9); and some head bones with weakly honeycombed surface (character 10). Two other characters provide equivocal support for monophyly of the genus (see

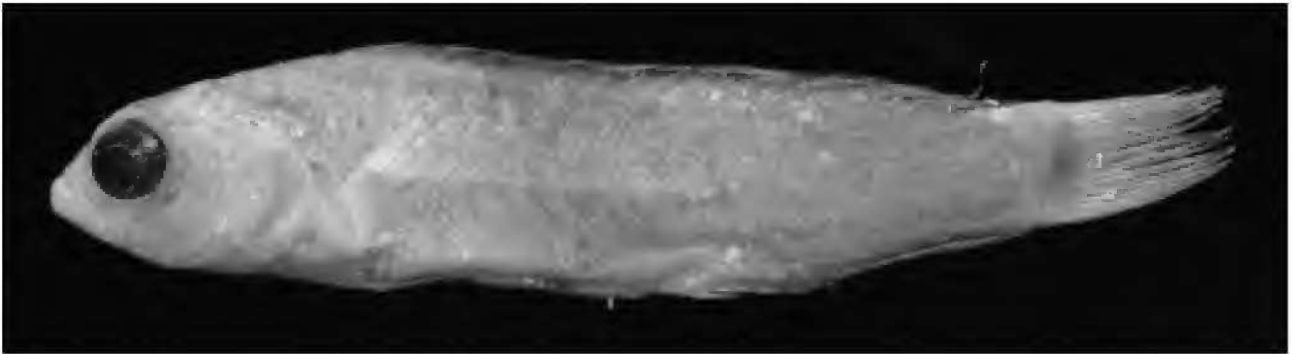


Figure 1. *Lubbockichthys multisquamatus*, WAM P.27470-002, 41.7 mm SL, holotype, Escape Reef, Great Barrier Reef.

Results of Parsimony Analysis below). The first of these, posterior interorbital pore present (character 23, state 0), is either an autapomorphy of *Lubbockichthys*, or diagnoses (state 1) a clade consisting of *Chlidichthys*, *Amsichthys*, *Pectinochromis* and *Pseudoplesiops*. The second character, dorsal-fin rays mostly branched (character 31, state 1), has three equally parsimonious optimisations on the proposed phylogeny, one of which optimises mostly branched rays as an autapomorphy of *Lubbockichthys* (and homoplastically of *Pectinochromis*). Other characters useful in identifying *Lubbockichthys* are summarised in Table 2.

Included nominal species. *Pseudoplesiops multisquamatus* Allen, 1987.

Geographic distribution. Eastern Indian Ocean to the central Pacific, from the Cocos-Keeling Islands, east to the Line Islands, south to New Caledonia and north to the Ryukyu Islands.

Justification for erection of new genus. Erection of *Lubbockichthys* is justified because it establishes a monophyletic classification; species assigned to *Lubbockichthys* cannot be assigned to any other pseudoplesiopine genus without rendering that genus para- or polyphyletic. The

erection of *Lubbockichthys* also draws attention to the morphological distinctiveness of the genus (and thus acknowledges a morphological gap).

Etymology. Named for the late Dr Hugh Roger Lubbock, in combination with the Greek *ichthys*, meaning fish, in recognition of Dr Lubbock's contributions to the systematics of pseudochromid fishes. Gender is masculine.

Pseudoplesiops Bleeker

Figs. 2, 9B, 10B, 11B, 12B, 13B, 14B

Pseudoplesiops Bleeker, 1858: 215 (type species, *Pseudoplesiops typus* Bleeker, by monotypy).

Nematochromis Weber, 1913: 264 (type species, *Nematochromis annae* Weber, by monotypy).

Diagnosis. *Pseudoplesiops* is demonstrably monophyletic in having the medial laminae of the pelvic bones expanded dorsally (character 11). Other characters useful in identifying the genus are summarised in Table 2.

Included nominal species. *Nematochromis annae* Weber, 1913; *Pseudoplesiops collare* Gill, Randall & Edwards, 1991; *P. howensis* Allen, 1987; *P. revellei* Schultz, 1953; *P.*



Figure 2. *Pseudoplesiops typus*, WAM P.30842-019, 54.6 mm SL, Ashmore Reef, Timor Sea.

rosae Schultz, 1943; *P. sargenti* Schultz, 1953; *P. typus* Bleeker, 1858.

Geographic distribution. Central Indian Ocean to the central Pacific, from the Maldive Islands, east to Oeno Atoll, north to the Ryukyu Islands and south to Lord Howe Island.

Etymology. From the Greek *pseudos*, false, and *Plesiops*, a genus of plesiopid fish, alluding to the purported similarity between the type species, *P. typus*, and *Plesiops*. Gender is masculine.

Amsichthys n.gen.

Figs. 3, 9C, 10C, 11A, 12C, 13C, 14C

Type species. *Pseudoplesiops knighti* Allen, 1987.

Diagnosis. *Amsichthys* is demonstrably monophyletic in lacking the upper preopercular pore (character 12). Monophyly of the genus is also supported by a single homoplastic character that also occurs in *Pectinochromis*: eyes large (character 30; see *Results of Parsimony Analysis* below). Other characters useful in identifying the genus are summarised in Table 2.

Included nominal species. *Pseudoplesiops knighti* Allen, 1987.

Geographic distribution. Eastern Indian Ocean and West Pacific, from the west coast of Thailand, east to the Solomon Islands, south to the Great Barrier Reef and north to the Ryukyu Islands.

Justification for erection of new genus. Our current hypothesis of generic relationships of pseudoplesiopines places *Amsichthys* as the sister group of *Pseudoplesiops*. Thus, it could be included within *Pseudoplesiops* without affecting the monophyletic status of that genus. However, we believe that character evidence for a sister relationship between the two genera is weak; such a relationship is supported by a single character, third supraneural bone well developed (character 25, state 1), but this varies among *Pseudoplesiops* species and intraspecifically in a *Chlidichthys* species (see *Results of Parsimony Analysis*). It is possible

that additional characters might lead to a different phylogenetic position for *Amsichthys*; indeed, a different interpretation of characters 12 and 28, such that the reduction in number of preopercular pores was seen as homologous, would lead to *Chlidichthys* + *Pectinochromis* forming the sister of *Amsichthys*. We therefore believe that the erection of *Amsichthys* will ultimately lead to greater nomenclatural stability, as its placement as the sister to any other pseudoplesiopine genus or clade of genera will not affect the generic assignment of its constituent species.

Erection of *Amsichthys* is also partly justified on the basis of its morphological distinctiveness.

Etymology. The generic name is a combination of AMS, the standard institutional code in ichthyology for the Australian Museum, Sydney, and the Greek *ichthys*, fish. It acknowledges the generous help, encouragement and friendship given by staff of the Australian Museum's Ichthyology Section to the first author during this study and throughout his career and training. Gender is masculine.

Chlidichthys Smith

Figs. 4, 6B, 7B, 8B, 9D, 10D, 12D, 13D, 14D

Chlidichthys Smith, 1953: 518 (type species: *Chlidichthys johnvoelckeri* Smith, 1953, by monotypy).

Wamizichthys Smith, 1954: 205 (type species: *Wamizichthys bibulus* Smith, 1954, by original designation and monotypy).

Diagnosis. *Chlidichthys* is distinguished from other pseudoplesiopines and demonstrably monophyletic in having two autapomorphies: lower lip interrupted at symphysis (character 13); and second infraorbital bone absent (character 26, state 2). Two other characters, 31 (state 0; mostly unbranched dorsal-fin rays) and 32 (state 1; mostly unbranched anal-fin rays), provide equivocal support for monophyly of the genus (see *Results of Parsimony Analysis* below). Other characters useful in identifying the genus are summarised in Table 2.

Included nominal species. *Chlidichthys abruptus* Lubbock, 1977; *C. auratus* Lubbock, 1975; *Wamizichthys bibulus* Smith, 1954; *C. cacatuoides* Gill & Randall, 1994; *C. inornatus* Lubbock, 1976; *C. johnvoelckeri* Smith, 1953;



Figure 3. *Amsichthys knighti*, NTM S.11384-018, North Reef, Timor Sea.



Figure 4. *Chlidichthys johnvoelckeri*, CAS 35451, 45.7 mm SL, Grande Comore Island, Comoro Islands.

C. pembae Smith, 1954; *C. randalli* Lubbock, 1977; *C. rubiceps* Lubbock, 1975; *C. smithae* Lubbock, 1977.

Geographic distribution. Western Indian Ocean, from the northern Red Sea and east Africa, north to southern Oman, east to Sri Lanka and south to Natal, South Africa.

Etymology. Apparently from the Greek *chlidanos*, delicate or luxurious, and *ichthys*, fish. Gender is masculine.

***Pectinochromis* n.gen.**

Figs. 5, 9E, 10E, 12E, 13E, 14E

Type species. *Pseudoplesiops lubbocki* Edwards & Randall, 1983.

Diagnosis. *Pectinochromis* is distinguished from other pseudoplesiopine genera and demonstrably monophyletic in having six autapomorphies: first dorsal-fin pterygiophore expanded anteriorly (character 14); first dorsal-fin pterygiophore with lateral processes (character 15); second pterygiophore of dorsal fin inserts between neural spines 3 and 4 (character 16); dorsal fin anteriorly positioned (character 17); single supraneural bone (character 18); gill rakers relatively numerous (character 19). Monophyly of the genus is also supported by a single homoplastic character, eyes large (character 30), that also occurs in *Amsichthys*. Another

homoplastic character, dorsal-fin rays mostly branched (character 31, state 1), has three equally parsimonious character optimisations within the Pseudoplesiopinae; two of the optimisations identify it as an autapomorphy of *Pectinochromis*. The presence of mostly branched anal-fin rays (character 32) also provides equivocal support for monophyly of the genus (see *Results of Parsimony Analysis* below for discussion of this and the previous two characters). Other characters useful in identifying the genus are summarised in Table 2.

Included nominal species. *Pseudoplesiops lubbocki* Edwards & Randall, 1983.

Geographic distribution. Red Sea.

Justification for erection of new genus. Our current hypothesis of generic relationships of pseudoplesiopines places *Pectinochromis* as the sister group of *Chlidichthys*; this relationship is strongly supported by five synapomorphies (see *Results of Parsimony Analysis* below). Thus, *Pectinochromis* could be included within *Chlidichthys* without affecting the monophyletic status of that genus. However, our decision to erect *Pectinochromis* is to draw attention to the morphological distinctiveness of the two genera. *Pectinochromis* is particularly distinctive, and is readily distinguished from all other pseudochromids by its unusual dorsal-fin and gill-raker morphology.

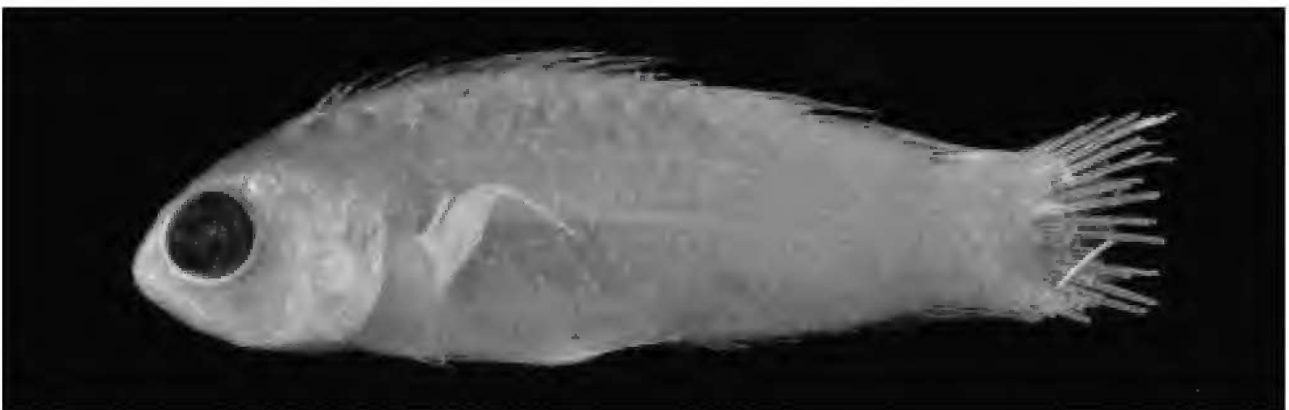


Figure 5. *Pectinochromis lubbocki*, BMNH 1982.6.9.1-4, 32.2 mm SL, Gulf of Aqaba, Red Sea.

Table 1. Matrix of 32 characters of pseudoplesiopine genera (see text for details of characters).

	character number																															
	1					2					3																					
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2										
outgroup	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	?	0
<i>Lubbockichthys</i>	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>Pseudoplesiops</i>	1	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	1
<i>Amsichthys</i>	1	1	1	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	1	0	1
<i>Chlidichthys</i>	1	1	1	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	0	1	2	1	1	1	0	0	1
<i>Pectinochromis</i>	1	1	1	1	1	1	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	0

Etymology. The generic name is from the Latin *pecten*, a comb or rake, and the Greek *Chromis*, a genus of pomacentrid fish, which has been used as a suffix for various pseudochromid genera (e.g., *Pseudochromis* and *Nematochromis*), and alludes to the relatively high number of gill rakers. Gender is feminine, in keeping with the accepted gender of *Chromis* [see Opinion 1417 (International Commission on Zoological Nomenclature, 1986) for ruling on the gender of *Chromis*].

Phylogenetic relationships

Character descriptions. A summary of character state distributions is given in Table 1.

Character 1. Single tubed anterior lateral-line scale. Pseudochromines and anisochromines have a series of tubed scales in the anterior portion of the lateral line (state 0). Pseudoplesiopines usually have only a single tubed scale, which is situated near the branchial opening (state 1; occasional specimens of *Lubbockichthys* species may have two tubed scales on one or both sides of the body). Congrogadines vary somewhat in the structure of their lateral line, but most have a single, anterodorsal lateral line consisting of a series of tubed scales (exceptions are *Rusichthys*, which lacks a lateral line, *Halidesmus*, which has three lateral lines, and *Halimuraenoides*, some *Halimuraena* species, one *Haliophis* species and occasional specimens of some *Congrogadus* species, all of which have two lateral lines, one anterodorsal, the other midlateral). The state found in pseudoplesiopines is regarded as apomorphic.

Character 2. Posterior part of pelvic bone with triangular or hook-shaped lateral process. Pseudochromines, anisochromines and congrogadines lack lateral processes on the posterior part of the pelvic bone (state 0; Fig. 6A). Pseudoplesiopines have a triangular or hook-shaped lateral process on the posterior part of the pelvic bone, which serves as an attachment site for a slip of hypaxial musculature (state 1; Fig. 6B). This arrangement is regarded as apomorphic.

Character 3. Base of anterior process on pelvic bone posteriorly positioned. The base of the anterior process (sensu Stiassny & Moore, 1992) of the pelvic bone of pseudochromines and anisochromines is positioned slightly to well anterior to the anterior edge of the pelvic-fin spine base (Fig. 6A; state 0). Congrogadines examined by us lack

an anterior process on the pelvic bone. In pseudoplesiopines, the anterior process is positioned noticeably posterior to the anterior edge of pelvic-fin spine base (Fig. 6B; state 1). The latter state is regarded as apomorphic.

Character 4. Coracoid articulates ventrally with medial face of lateral lamina of cleithrum. In pseudochromines, anisochromines and congrogadines the ventral process of the coracoid attaches to the lateral face of a medial lamina on the cleithrum (Fig. 7A; state 0), whereas in pseudoplesiopines the coracoid attaches to the medial face of a lateral lamina (Fig. 7B; state 1). The latter state is regarded as apomorphic.

Character 5. Basihyal bound to anterior face of basibranchial 1. The basihyal loosely overlies basibranchial 1 in pseudochromines and anisochromines (Fig. 8A,C; state 0). It is tightly bound by connective tissue to the anterior face of basibranchial 1 in pseudoplesiopines (Fig. 8B; state 1). The basihyal is bound more-or-less tightly to basibranchial 1 in congrogadines (Fig. 8D), but the arrangement does not appear to be homologous with the condition found in pseudoplesiopines. Most notably, the condition in congrogadines differs in that there are two articulation points between the two bones, a dorsal attachment between the mid-dorsal face of basibranchial 1 and the posterior tip of the basihyal, and a ventral attachment between the anterior (cartilaginous) tip of basibranchial 1 and the posteroventral edge of the basihyal. In the latter attachment, the basihyal is embraced by small lateral projections that extend anteriorly from basibranchial 1 (and obscure the anterior cartilage tip from lateral view). The congrogadine condition is associated with a very different arrangement of the basibranchial 1/urohyal articulation, where the urohyal is positioned farther posteriorly (as it is also in anisochromines), articulating with a posteroventral process from basibranchial 1 (versus weakly associated with the anterior cartilage tip of basibranchial 1 in pseudochromines and pseudoplesiopines). We consider the basihyal/basibranchial 1 arrangement displayed by pseudoplesiopines to be apomorphic within the Pseudochromidae.

Character 6. Urohyal with prominent dorsally directed process. The urohyal of pseudochromines has a small to moderately developed posterodorsally directed process, which is weakly embraced by anteroventrally projecting processes from the hypobranchials 1 (Fig. 8A; state 0).

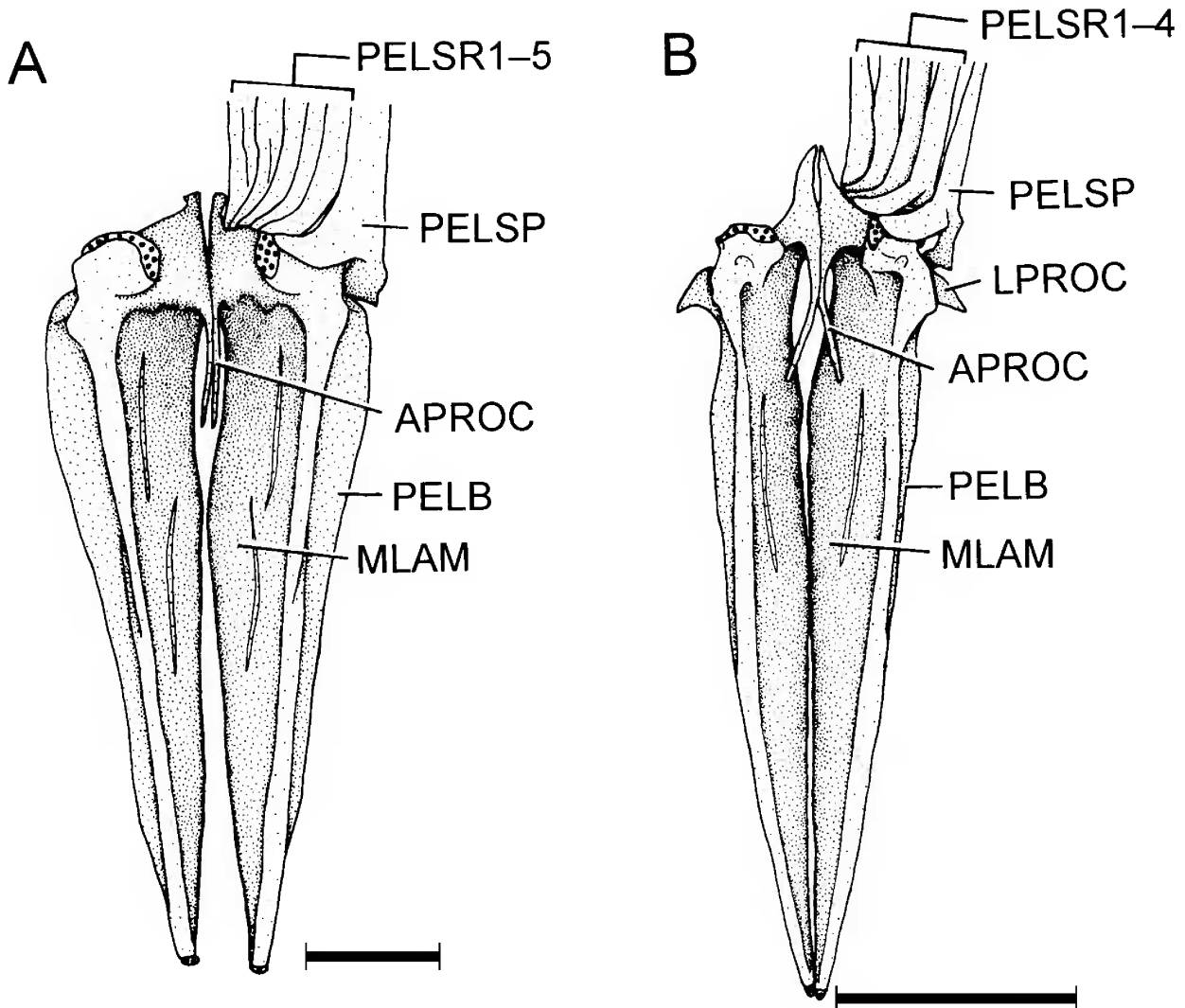


Figure 6. Pelvic girdles of two pseudochromid species in ventral view: A, "*Pseudochromis*" cf. *paccagnellae* (Pseudochrominae), AMS I.22613-008, 46.2 mm SL; B, *Chlidichthys johnvoelckeri* (Pseudoplesiopinae), CAS 35451, 37.9 mm SL. Anterior to bottom of page; cartilage shown in large stipple. Abbreviations: APROC, anterior process; LPROC, lateral process; MLAM, medial lamina; PELB, pelvic bone; PELSP, pelvic-fin spine; PELSR1-5, pelvic segmented rays 1-5. Scale bars = 1 mm.

Pseudoplesiopines have a prominent dorsal process on the urohyal, which is also embraced by anteroventral processes from the hypobranchials 1, but it is dorsally rather than posterodorsally directed (Fig. 8B; state 1). Anisochromines and congrogadines lack a dorsal process from the urohyal to the hypobranchials 1; the urohyal is well separated from the hypobranchials, and the hypobranchials have small posteroventrally (rather than anteroventrally) projecting processes (Fig. 8C,D). The condition shown by pseudoplesiopines is considered apomorphic within the Pseudochromidae.

Character 7. Parietal bears enclosed lateral-line canal. In *Chlidichthys*, *Amsichthys*, *Pectinochromis* and most *Pseudoplesiops*, the dorsal portion of the supratemporal lateral-line commissure passes over the parietal as a membranous canal, which is either unossified or ossified medially only (Fig. 9B-E; state 0). In *Lubbockichthys* and

Pseudoplesiops howensis, the dorsal portion of the supratemporal lateral-line commissure passes through a fully ossified (enclosed) canal in the parietal (Fig. 9A; state 1). In *Assiculoides* and *Assiculus*, the supratemporal commissure passes over the parietal in a membranous tube that is either unossified or medially ossified only; anisochromines have similar ossification of the canal, but the commissure is heavily branched and continuous across the dorsal midline. In congrogadines, the commissure is also continuous across the dorsal midline, but is mostly ossified throughout its length. As far as we can ascertain, the ossified portion is separate from, though closely applied to, the parietal bone. We therefore consider the condition shown by *Lubbockichthys* and *P. howensis* apomorphic.

Character 8. Scales "cycloid" at all stages of ontogeny. *Chlidichthys*, *Amsichthys*, *Pectinochromis* and *Pseudoplesiops* have cteni on posterior body scales, at

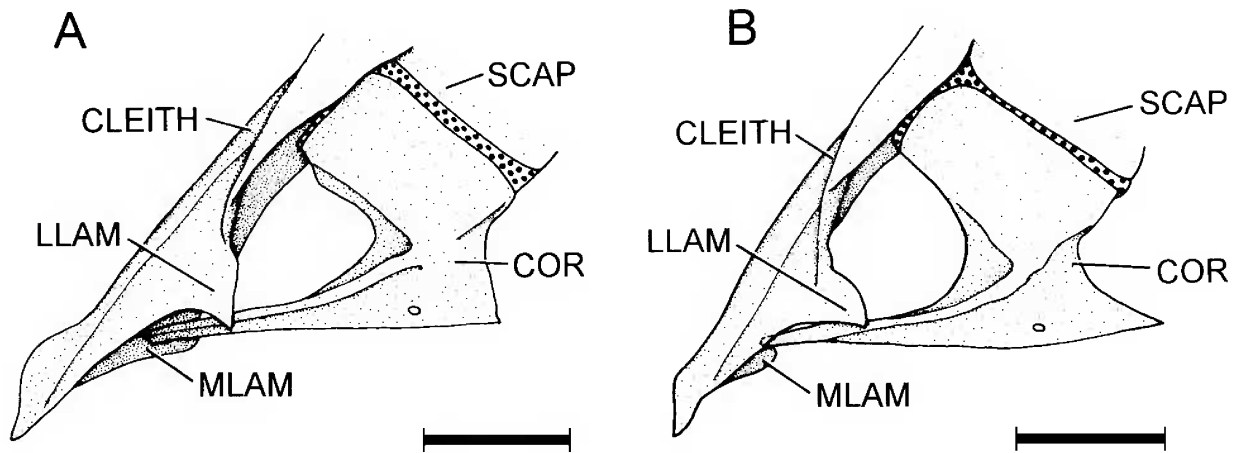


Figure 7. Right lateral view (reversed) of lower part of pectoral girdle of two pseudochromid species: A, *“Pseudochromis” diadema* (Pseudochrominae), USNM 210017, 35.0 mm SL; B, *Chlidichthys johnvoelckeri* (Pseudoplesiopinae), CAS 35451, 37.9 mm SL. Abbreviations: CLEITH, cleithrum; COR, coracoid; MLAM, medial lamina of cleithrum; LLAM, lateral lamina of cleithrum; SCAP, scapula. Scale bars = 1 mm.

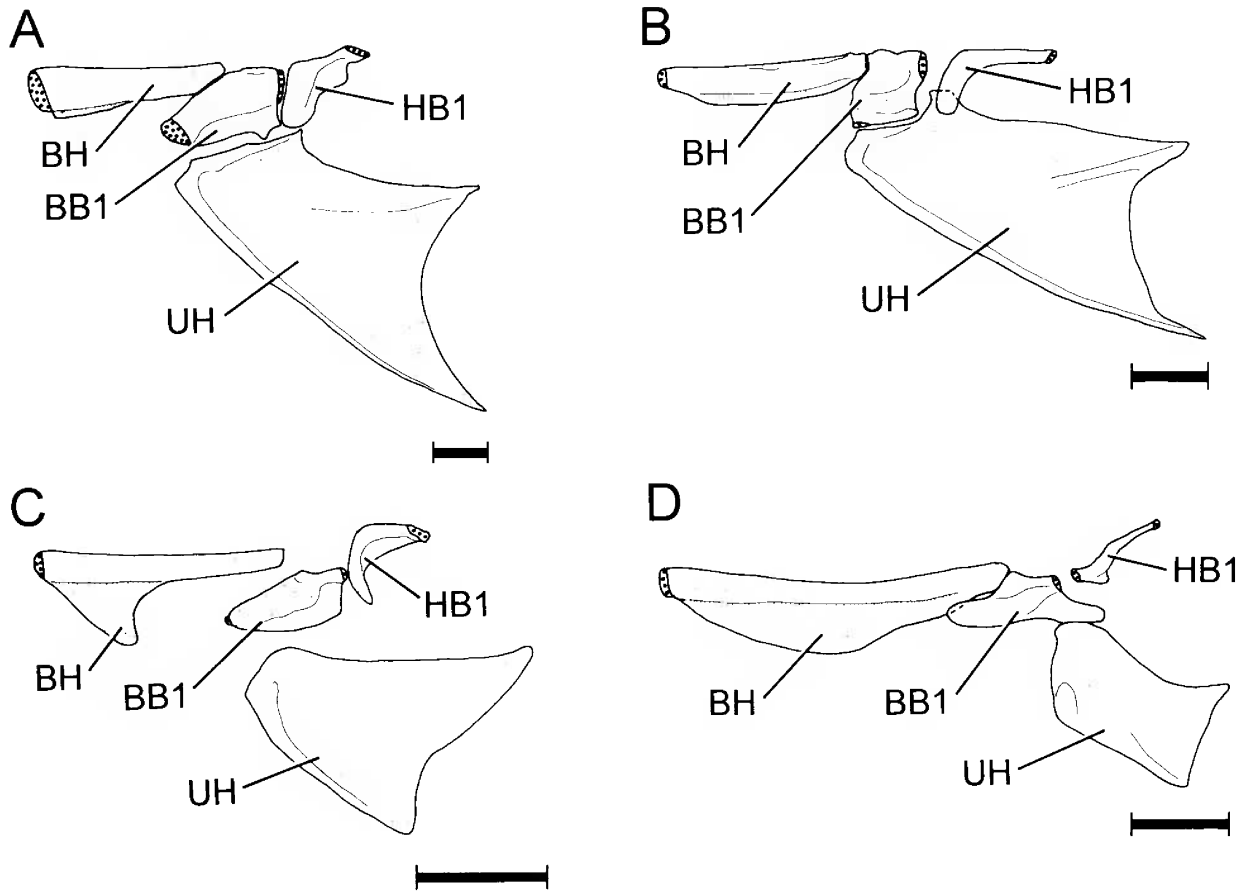


Figure 8. Right lateral view (reversed) of basihyal (BH), basibranchial 1 (BB1), hypobranchial 1 (HB1) and urohyal (UH) of selected pseudochromid species: A, *Assiculus punctatus* (Pseudochrominae), NTM S.10016-009, 32.2 mm SL; B, *Chlidichthys johnvoelckeri* (Pseudoplesiopinae), CAS 35451, 37.9 mm SL; C, *Anisochromis kenya* (Anisochrominae), RUSI 4906, 23.3 mm SL; D, *Blennodesmus scapularis* (Congrogadinae), AMS I.26723-087, 49.7 mm SL. Cartilage shown in large stipple. Scale bars = 0.5 mm.

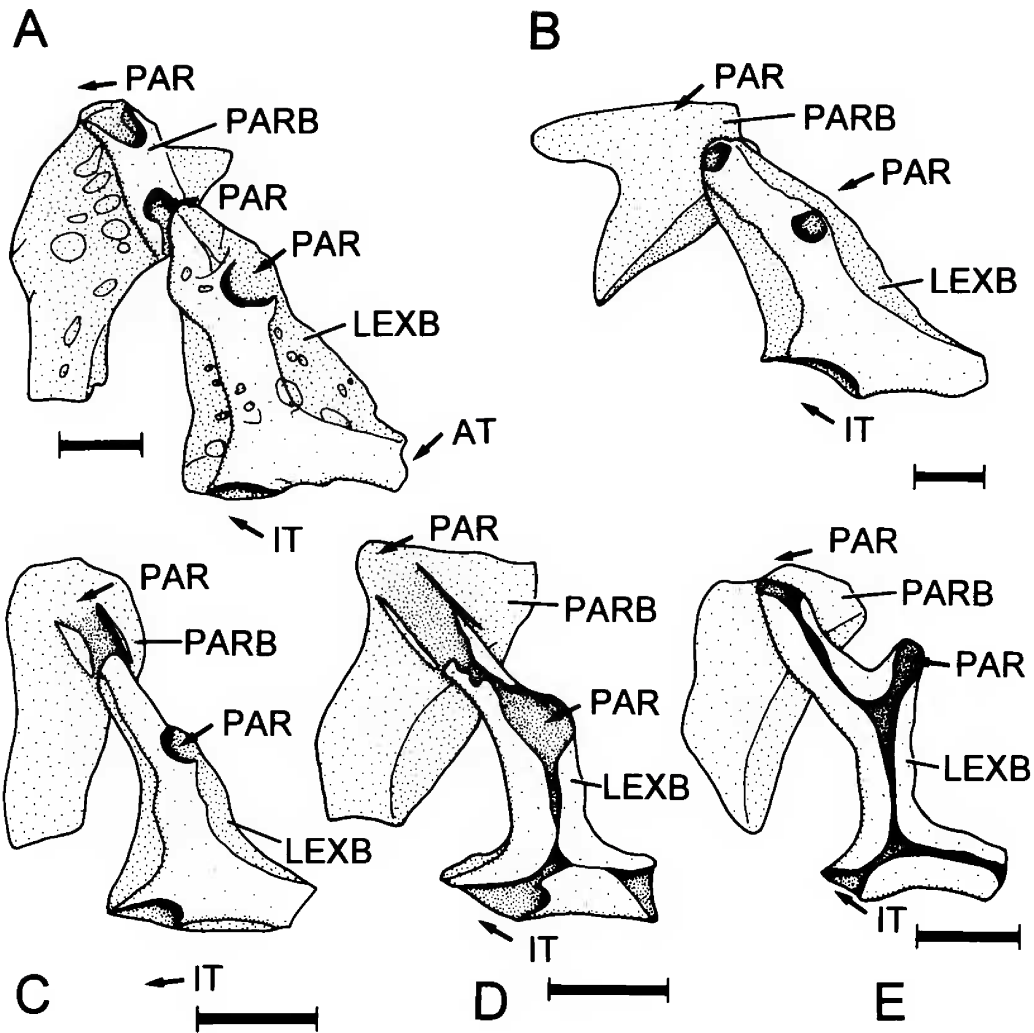


Figure 9. Lateral extrascapulae and parietal bones and associated laterosensory pores of selected pseudoplesiopsine species: A, *Lubbockichthys* sp. 1, AMS I.25107-067, 47.3 mm SL; B, *Pseudoplesiops typus*, AMS I.19442-013, 50.6 mm SL; C, *Amsichthys knighti*, AMS I.22612-034, 28.3 mm SL; D, *Chlidichthys johnvoelckeri*, CAS 35451, 37.9 mm SL; E, *Pectinochromis lubbocki*, BPBM 28119, 35.5 mm SL (paratype). Arrows indicate locations of sensory pores. Abbreviations: AT, anterior temporal pore; IT, intertemporal pore; LEXB, lateral extrascapular bone; PAR, parietal pore; PARB, parietal bone. Scale bars = 0.5 mm.

least as juveniles (state 0), as do pseudochromines and anisochromines and the vast majority of perciforms. Species of *Lubbockichthys* are unique among pseudoplesiopsines in lacking cteni on body scales at all stages of ontogeny (state 1). The posterior body scales of congrogadines also lack cteni, as do those of some perciform taxa, such as ambassids, bathyclupeids, carangoids, cepolids, dinolestids, lactariids, leiognathids, opistognathids, siniperoids, clinids, dactyloscopids, zoarcoids, and most cirrhitoids (see Johnson, 1984: table 120; Roberts, 1993: appendix 1). Such scales have been generally termed "cycloid", but they are not homologous with the cycloid scales of lower teleosts (J. Radding, pers. comm.). Cteni are present in small (less than about 30 mm SL) specimens of *Pseudoplesiops typus*, but are absent from larger specimens; presumably cteni are either shed or, more likely, resorbed with growth. Other species of

Pseudoplesiops retain cteni on posterior body scales throughout ontogeny. We regard the condition found in *Lubbockichthys* as apomorphic and nonhomologous with that found in *P. typus*.

Character 9. Scales small. *Chlidichthys*, *Amsichthys*, *Pectinochromis* and *Pseudoplesiops* have relatively large to moderately small scales (state 0). In contrast, *Lubbockichthys* has relatively small scales (state 1). This character can be seen by differences in numbers of scales in lateral series (Table 2): 37–52 in *Chlidichthys*, 30–33 in *Amsichthys*, 35–39 in *Pectinochromis* and 26–42 in *Pseudoplesiops*, versus 51–66 in *Lubbockichthys*. Most of the outgroup taxa have relatively large to moderately small scales. Scales in lateral series counts range from 39–44 in anisochromines, 35–42 in *Assiculoides*, and 38–46 in *Assiculus*. However, congrogadines also have numerous, small scales. Nevertheless,

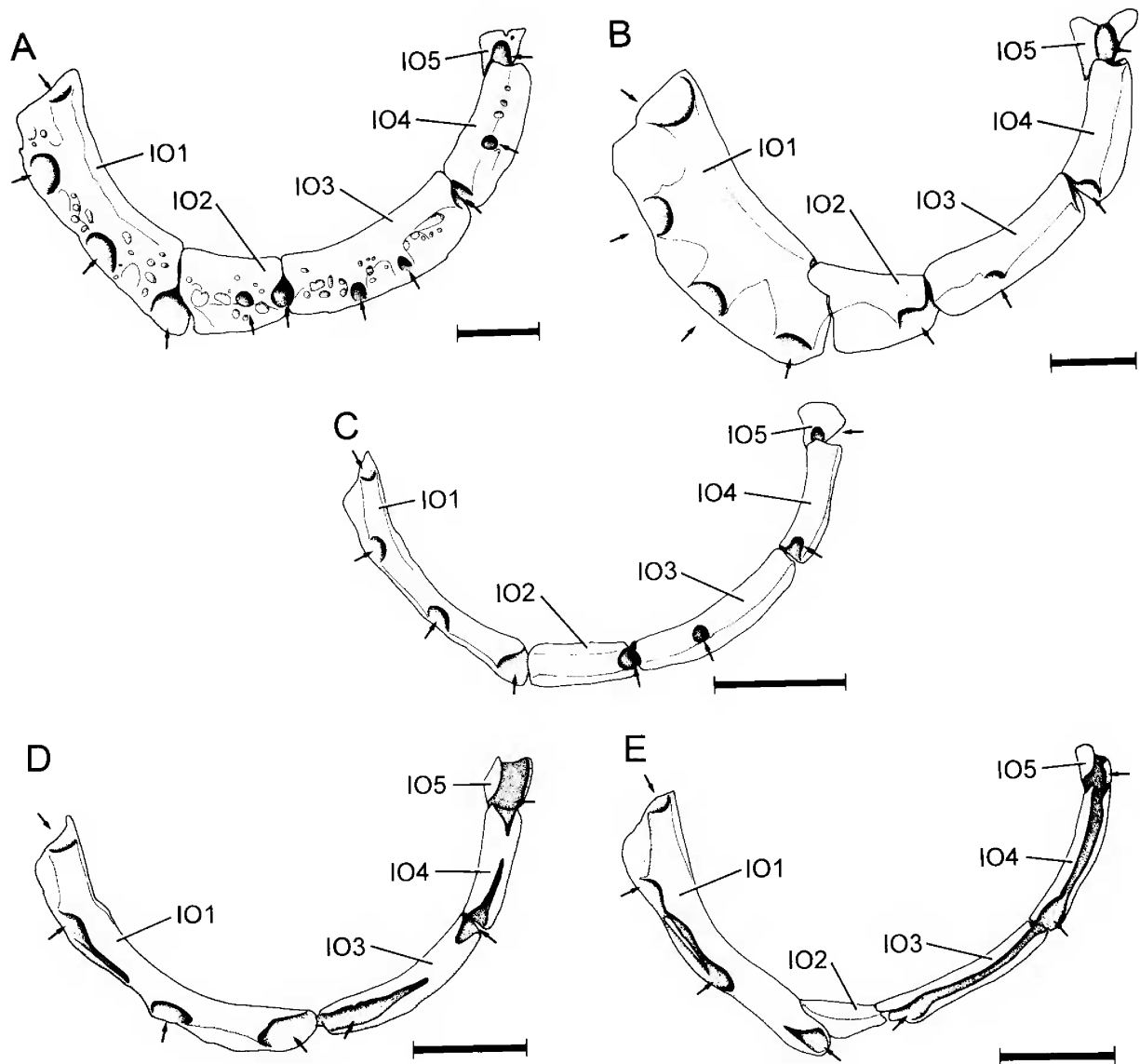


Figure 10. Infraorbital bones (IO1-5) of selected pseudoplesiopine species in left lateral view: A, *Lubbockichthys* sp. 1, AMS I.25107-067, 47.3 mm SL; B, *Pseudoplesiops typus*, ROM CS585, 49.0 mm SL; C, *Amsichthys knighti*, AMS I.22612-034, 28.3 mm SL; D, *Chlidichthys johnvoelckeri*, CAS 35451, 37.9 mm SL; E, *Pectinochromis lubbocki*, BPBM 28119, 35.5 mm SL (paratype). Arrows indicate positions of suborbital pores. Scale bars = 1 mm.

the condition shown by *Lubbockichthys* is most parsimoniously argued to be derived within the Pseudoplesiopinae.

Character 10. Some head bones with weakly honeycombed surface. *Pseudoplesiops*, *Amsichthys*, *Pectinochromis* and *Chlidichthys* have relatively smooth head bones (e.g., Figs. 9B-E, 10B-E; state 0), as do the outgroup taxa. *Lubbockichthys* has at least some head bones with a weakly honeycombed surface (e.g., Figs. 9A, 10A; state 1). We consider this condition to be apomorphic within the Pseudoplesiopinae.

Character 11. Medial laminae of pelvic bones expanded dorsally. The medial laminae (= inner wing of Stiassny & Moore, 1992) of the pelvic bones of *Lubbockichthys*,

Amsichthys, *Chlidichthys* and *Pectinochromis* are at most weakly expanded dorsally, so that the pelvic bones have a concave to weakly convex dorsal profile (Fig. 11A; state 0). The medial laminae of the pelvic bones of *Pseudoplesiops* are strongly expanded dorsally, so that the bones have a strongly convex dorsal profile (Fig. 11B; state 1). Anisochromines and the basal congrogadine genus *Rusichthys* have dorsally expanded medial laminae (with the exception of *Halidesmus scapularis*, more derived congrogadine genera lack dorsally expanded medial laminae, but this appears to be associated with reduction or loss of the pelvic fin), whereas *Assiculoides* and *Assiculus* (and all other pseudochromines) have weakly expanded laminae on the pelvic bones. Because both states occur in the outgroup taxa, this character was not polarised.

Character 12. Loss of uppermost preopercular pore. *Lubbockichthys*, *Pseudoplesiops*, *Pectinochromis* and *Chlidichthys* and the outgroup taxa have the uppermost preopercular pore associated with the terminal opening in the preopercle (Fig. 12A,B,D,E; state 0). *Amsichthys* is distinctive in usually lacking a pore at the dorsal terminus of the preopercle (Fig. 12C; state 1). We consider the absence of the dorsal pore apomorphic. A terminal pore was present on one or both sides of the head of a few, relatively large specimens of *Amsichthys*; in contrast, a terminal pore was consistently present in juveniles and adults of the other pseudoplesiopine genera and in the outgroups. This suggests that the pore may develop relatively late in ontogeny in *Amsichthys*, in which case the character should be redescribed as delayed development of uppermost preopercular pore rather than loss of uppermost preopercular pore.

Character 13. Lower lip interrupted at symphysis. *Amsichthys*, *Lubbockichthys*, *Pectinochromis*, *Pseudoplesiops*, anisochromines, congrogadines, *Assiculoides* and *Assiculus* have the lower lip uninterrupted at the symphysis (Gill & Randall, 1994: fig. 1A; Gill & Hutchins, 1997: fig. 4; state 0). *Chlidichthys* species are unique among pseudoplesiopines in having the lower lip interrupted at the symphysis (Gill & Randall, 1994: fig. 1B; state 1). We consider the latter condition apomorphic.

Character 14. First dorsal-fin pterygiophore expanded anteriorly. The anterior face of the first dorsal-fin pterygiophore is at best weakly expanded anteriorly in *Chlidichthys*, *Amsichthys*, *Lubbockichthys* and *Pseudoplesiops* (Fig. 13A–D; state 0). *Pectinochromis* is unusual in having the anterior part of the first dorsal-fin pterygiophore strongly expanded anteriorly (Fig. 13E; state 1). Anisochromines, *Assiculoides* and *Assiculus* have the anterior face of the first pterygiophore

weakly expanded anteriorly; congrogadines lack the homologue of the first dorsal-fin pterygiophore (Gill, 1998). We therefore consider the condition shown by *Pectinochromis* apomorphic.

Character 15. First dorsal-fin pterygiophore with lateral processes. *Chlidichthys*, *Amsichthys*, *Lubbockichthys* and *Pseudoplesiops* lack lateral processes on the first dorsal-fin pterygiophore (Fig. 13A–D; state 0). *Pectinochromis* is distinctive in having prominent lateral processes on the first dorsal-fin pterygiophore (Fig. 13E; state 1). Anisochromines, *Assiculoides* and *Assiculus* lack such processes (and, as noted above, congrogadines lack the homologue of the first pterygiophore), and we therefore consider the condition shown by *Pectinochromis* apomorphic.

Character 16. Second dorsal-fin pterygiophore insertion between neural spines 2 and 3. *Chlidichthys*, *Amsichthys*, *Lubbockichthys*, *Pseudoplesiops*, anisochromines, *Assiculus* and *Assiculoides* have the first dorsal-fin pterygiophore insertion between neural spines 2 and 3, and the next two pterygiophores between neural spines 3 and 4 (Fig. 13A–D; state 0). Congrogadines have only two dorsal-fin pterygiophores inserting anterior to neural spine 4, both positioned between neural spines 3 and 4, owing to the loss of the first pterygiophore (Gill, 1998). *Pectinochromis* has the first two pterygiophores between neural spines 2 and 3, and the third pterygiophore between neural spines 3 and 4 (Fig. 13E; state 1). The anterior position of the second pterygiophore is regarded as apomorphic.

Character 17. Dorsal fin anteriorly positioned. The dorsal-fin origin of *Lubbockichthys*, *Pseudoplesiops*, *Amsichthys* and *Chlidichthys* is near the vertical through the posterior edge of the operculum (Figs. 1–4, 12A–D; state 0), as it is in the outgroup taxa. *Pectinochromis* is unusual in having the dorsal-

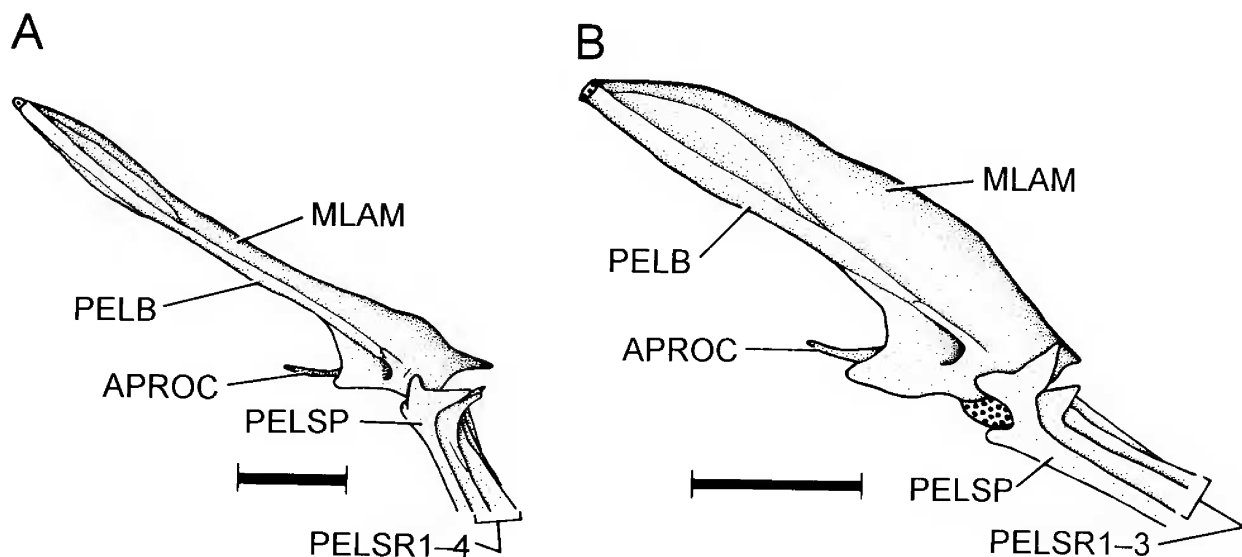


Figure 11. Right lateral view (reversed) of pelvic girdles of two pseudoplesiopine species: A, *Amsichthys knighti*, AMS I.22612-034, 28.3 mm SL; B, *Pseudoplesiops rosae*, AMS I.22582-073, 22.0 mm SL. Abbreviations as in Fig. 1. Cartilage shown in large stipple. Scale bars = 0.5 mm.

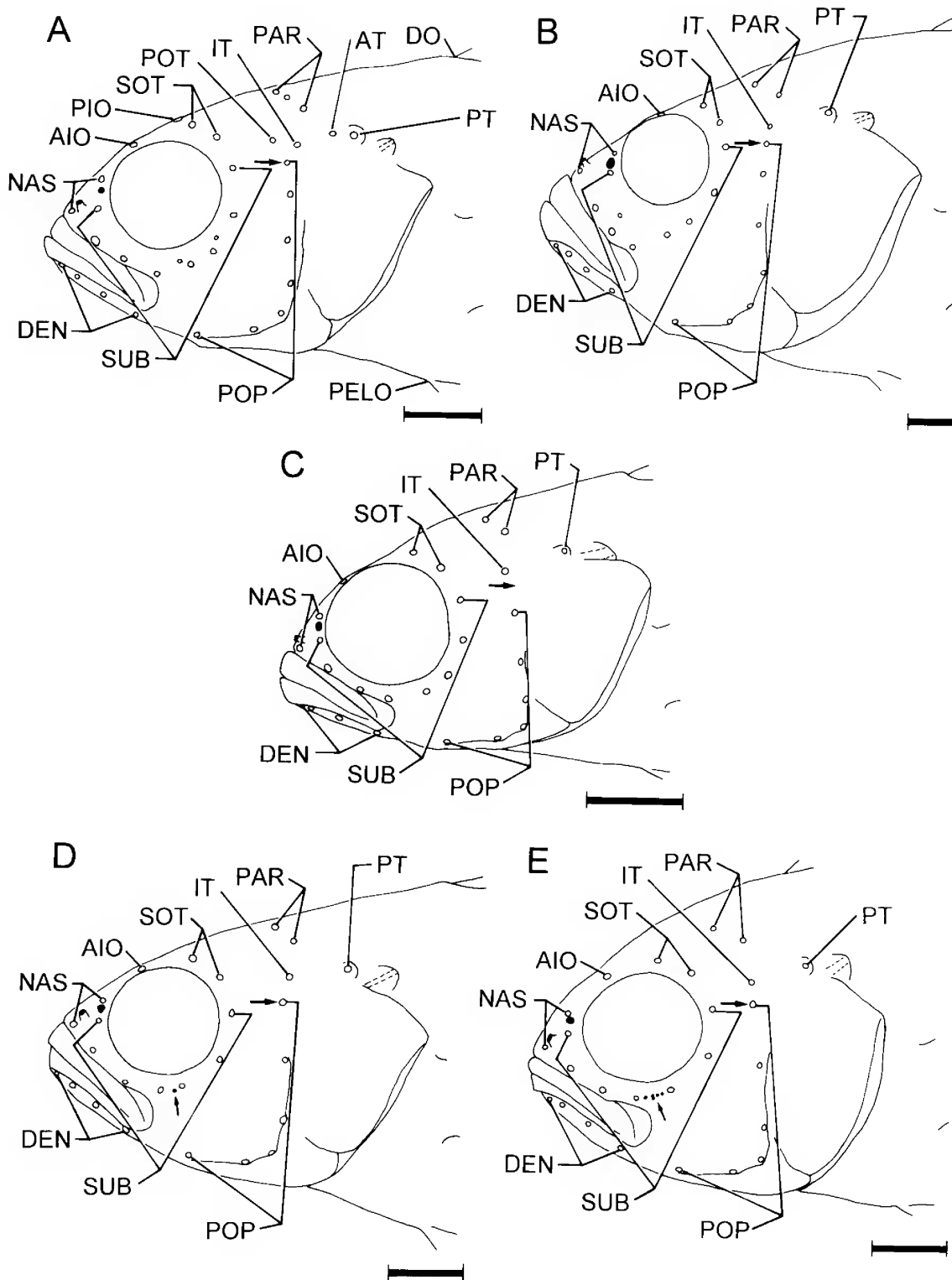


Figure 12. Left lateral diagrams of heads of selected pseudoplesiopine species: A, *Lubbockichthys multisquamatus*, AMS I.220779-175, 36.3 mm SL; B, *Pseudoplesiops typus*, WAM P.30842-019, 54.6 mm SL; C, *Amsichthys knightii*, NTM S.11384-018, 25.0 mm SL; D, *Chlidichthys johnvoelckeri*, ROM uncat., (field number RW 88-26), 36.2 mm SL; E, *Pectinochromis lubbocki*, BMNH 1982.6.9.1-4, 32.2 mm SL (paratype). Large arrow indicates dorsal tip of preopercle. Superficial neuromasts in D and E shown in black and indicated by small arrow. Abbreviations: AIO, anterior interorbital pore; AT, anterior temporal pore; DEN, dentary pores; DO, dorsal-fin origin; IT, intertemporal pore; NA, nasal pores; PLO, pelvic-fin origin; PAR, parietal pores; PIO, posterior interorbital pore; POP, preopercular pores; POT, posterior otic pore; PT, posttemporal pore; SOB, suborbital pores; SOT, supraotic pores. Scale bars = 2 mm.

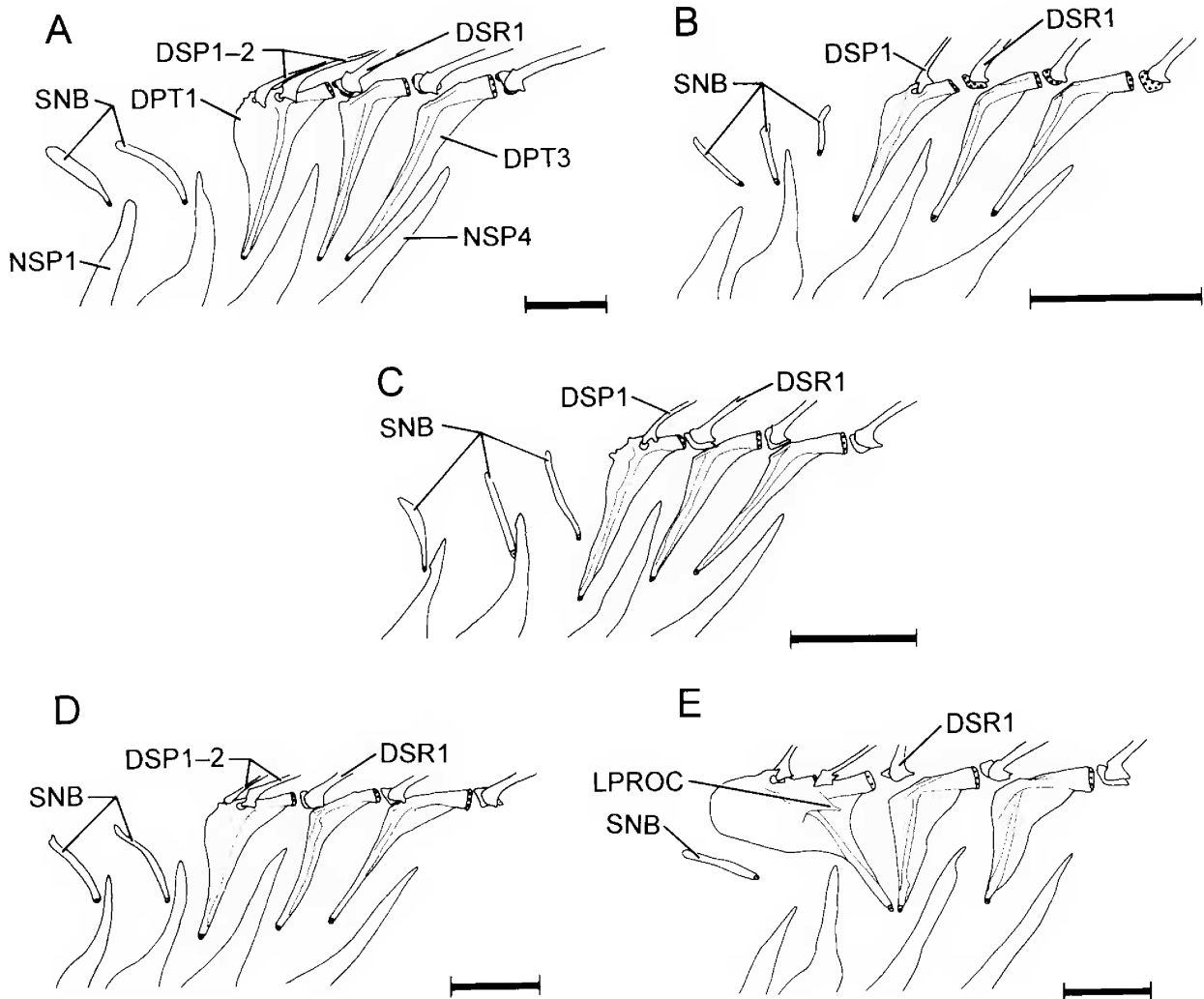


Figure 13. Anterior dorsal-fin pterygiophores and supraneural bones of selected pseudoplesiopine species in left lateral view: A, *Lubbockichthys* sp. 1, AMS L25107-067, 47.3 mm SL; B, *Pseudoplesiops howensis*, AMS L19755-024, 21.0 mm SL; C, *Amsichthys knighti*, AMS L22612-034, 28.3 mm SL; D, *Chlidichthys johnvoelckeri*, CAS 35451, 37.9 mm SL; E, *Pectinochromis lubbocki*, BPBM 28119, 35.5 mm SL (paratype). Cartilage shown in large stipple. Abbreviations: DPT1,3, dorsal-fin pterygiophores 1,3; DSP1-2, dorsal-fin spines 1-2; DSR1, segmented dorsal-fin ray 1; LPROC, lateral process on first dorsal-fin pterygiophore; NSP1,4, neural spines 1,4; SNB, supraneural bones. Scale bars = 1 mm.

fin origin near the vertical through the preopercle (Figs. 5, 7E; state 1), a condition that we consider apomorphic.

Character 18. Single supraneural bone. *Lubbockichthys*, *Pseudoplesiops*, *Amsichthys*, *Chlidichthys*, *Assiculoides*, *Assiculus* and anisochromines have more than one supraneural bone (Fig. 13A–D; state 0). *Pectinochromis* has a single supraneural bone (Fig. 13E; state 1). Congrogadines have one to three tiny supraneural bones, varying considerably within species. We regard the single supraneural in *Pectinochromis* apomorphic.

Character 19. Numerous outer first-gill-arch rakers. Most pseudoplesiopines have relatively low to moderate numbers of total rakers on the outer face of the first gill arch: 12–16 for *Amsichthys*; 9–17 for *Pseudoplesiops*; 12–19 for *Chlidichthys*; and 12–21 for *Lubbockichthys* (state 0). The outgroup taxa have similar low to moderate numbers: 3–9 in anisochromines;

6–17 in congrogadines; 14–18 in *Assiculoides*; and 13–17 in *Assiculus*. *Pectinochromis* is distinctive in having numerous rakers on the outer face of the first arch, ranging from 27–31 (state 1). This state is regarded as apomorphic.

Character 20. Segmented pelvic-fin rays all unbranched. Adult specimens of *Lubbockichthys* have one or more segmented pelvic-fin rays branched (state 0). *Chlidichthys*, *Amsichthys*, *Pectinochromis* and *Pseudoplesiops* have all segmented pelvic-fin rays unbranched, (state 1). With the exception of some congrogadines that lack pelvic fins, the outgroup taxa have one or more branched segmented rays in the pelvic fin. The absence of branched rays is therefore regarded as apomorphic.

Character 21. Posterior otic pores absent. Adult specimens of *Lubbockichthys* have one or more posterior otic pores on each side of the head (Fig. 12A; state 0). The remaining

pseudoplesiopine genera lack posterior otic pores (Fig. 12B–E; state 1). Posterior otic pores are present in *Assiculus*, *Assiculoides* and anisochromines, and are either present (*Halidesmus*, *Halimuraenoides* and *Congrogadus* (*Congrogadus*)) or absent (*Rusichthys*, *Haliophis*, *Natalichthys*, *Blennodesmus*, *Halimuraena* and *Congrogadus* (*Congrogadoides*)) in congrogadines (Winterbottom, 1986, 1996; Winterbottom & Randall, 1994). The lack of posterior otic pores is regarded as apomorphic within the Pseudoplesiopinae.

Character 22. Anterior temporal pores absent. Adult specimens of *Lubbockichthys* have an anterior temporal pore on each side of the head (Figs. 9A, 12A; state 0). The remaining pseudoplesiopine genera lack anterior temporal pores (Figs. 9B–E, 12B–E; state 1). *Assiculus*, *Assiculoides*, anisochromines and congrogadines possess anterior temporal pores; the absence of anterior temporal pores is therefore apomorphic within the Pseudoplesiopinae.

Character 23. Posterior interorbital pores. Adult specimens of *Lubbockichthys* have 1–2 (usually 1) median posterior interorbital pores on the head (Fig. 12A; state 0). The remaining pseudoplesiopine genera lack median posterior interorbital pores (Fig. 12B–E; state 1). *Assiculoides* and *Assiculus* lack median posterior interorbital pores. However, such pores are present in anisochromines and the majority of congrogadines. The polarity of this character within the Pseudoplesiopinae is, therefore, equivocal.

Character 24. Third supraneural bone well developed. The third supraneural bone is small or absent in *Lubbockichthys*, *Pectinochromis*, anisochromines, congrogadines, *Assiculoides*, *Assiculus* and all but one species of *Chlidichthys* (Fig. 13A,D,E; state 0). *Amsichthys* and all but a few relatively derived *Pseudoplesiops* species have the third supraneural bone well developed (Fig. 13B,C; state 1), a condition that we consider to be apomorphic. *Chlidichthys abruptus* is unique among pseudoplesiopines in exhibiting considerable intraspecific variation in this character; approximately one quarter of specimens examined lacked a third supraneural bone, whereas the remaining specimens had a weakly to well-developed third supraneural bone.

Character 25. Three epurals. *Lubbockichthys*, *Amsichthys* and *Pseudoplesiops* have two epurals (Fig. 14A–C; state 0), as do anisochromines, *Assiculoides* and basal congrogadines. *Chlidichthys* and *Pectinochromis* have three epurals (Fig. 14D,E; state 1). *Assiculus* and most of the remaining pseudochromines also have three epurals. [The exceptions, aside from *Assiculoides*, are members of the *Pseudochromis tapeinosoma* group (Gill & Allen, 1996), which have two epurals.] Taken in the context of the scheme of outgroup relationships proposed herein, the three-epural state is most parsimoniously interpreted as apomorphic among pseudoplesiopines.

Character 26. Infraorbital 2 reduced or absent. In *Lubbockichthys*, *Amsichthys* and *Pseudoplesiops*, the infraorbital branch of the cephalic lateral-line systems passes through an uninterrupted series of canals in the five infraorbital bones (Fig. 10A–C; state 0). In *Pectinochromis*,

infraorbital 2 is reduced in size and lacks a lateral-line canal, so that the canal passing through infraorbital 1 (lachrymal) does not communicate with the posterior series of canals (Fig. 10E; state 1). Infraorbital 2 is absent in *Chlidichthys*, giving a total of only four infraorbitals, and the canal passing through infraorbital 1 usually (see below) does not communicate with the posterior series of canals (Fig. 10D; state 2). The only *Chlidichthys* species in which there is communication between the anterior and posterior portions of the infraorbital canal (i.e., between infraorbitals 1 and 3) are the three members of a derived clade within the genus, *C. cacatuoides*, *C. inornatus* and *C. rubiceps*; we consider the uninterrupted series of infraorbitals in these species secondarily derived, and non-homologous with the outgroup condition. The outgroup taxa usually have the infraorbital branch of the cephalic lateral-line system passing through an uninterrupted series of canals in four (congrogadine genus *Natalichthys*), five (*Assiculoides*, anisochromines and most congrogadines) or six (*Assiculus*) infraorbital bones. (The noteworthy exception is the congrogadine genus *Rusichthys*, where only infraorbital bone 1 is present, and it does not communicate with the remainder of the cephalic lateral-line system.) Within the Pseudoplesiopinae, the reduction (through loss of the canal) and loss of infraorbital 2 are here regarded as an ordered transformation series. The reduction or loss of the second infraorbital in *Pectinochromis* and *Chlidichthys* is associated with the absence of a suborbital laterosensory pore that is present at the posterior opening of the second infraorbital in the remaining pseudoplesiopine genera. Instead, one or a series of superficial neuromasts are present between the tips of the first and third infraorbitals (Fig. 12D,E).

Character 27. Laterosensory-canal-bearing bones weakly developed. The laterosensory-canal-bearing bones of *Lubbockichthys*, *Pseudoplesiops* and *Amsichthys* are relatively well ossified, usually with well-developed laminar edges (Figs. 9A–C, 10A–C; state 0), as they are in the outgroup taxa (at least in adult specimens). In contrast, those of *Chlidichthys* and *Pectinochromis* are relatively weakly ossified, often with slit-like openings extending along the bones, and without well-developed laminar edges (Figs. 9D,E, 10D,E; state 1). We consider the latter apomorphic within the Pseudoplesiopinae.

Character 28. Second preopercular pore absent. *Lubbockichthys* has 6–11, rarely 6 (six only in small specimens) and *Pseudoplesiops* has 6–8, rarely 6 or 8, preopercular pores, with the upper two pores relatively closely spaced (Fig. 12A,B; state 0). *Pectinochromis* and *Chlidichthys* usually have only six preopercular pores (occasional specimens of both genera may have seven pores on one or both sides, but the configuration of upper pores is the same as in specimens with six pores), with the upper pore well separated from the lower pores (Fig. 12D,E; state 1). The relatively low number of pores is here argued to have resulted from the loss of the homologue of the second pore of the seven-pored genera, which results in the upper two pores being well separated from each other. *Amsichthys* also usually has only six pores (Fig. 12C), but the arrangement is here argued to be non-homologous with that

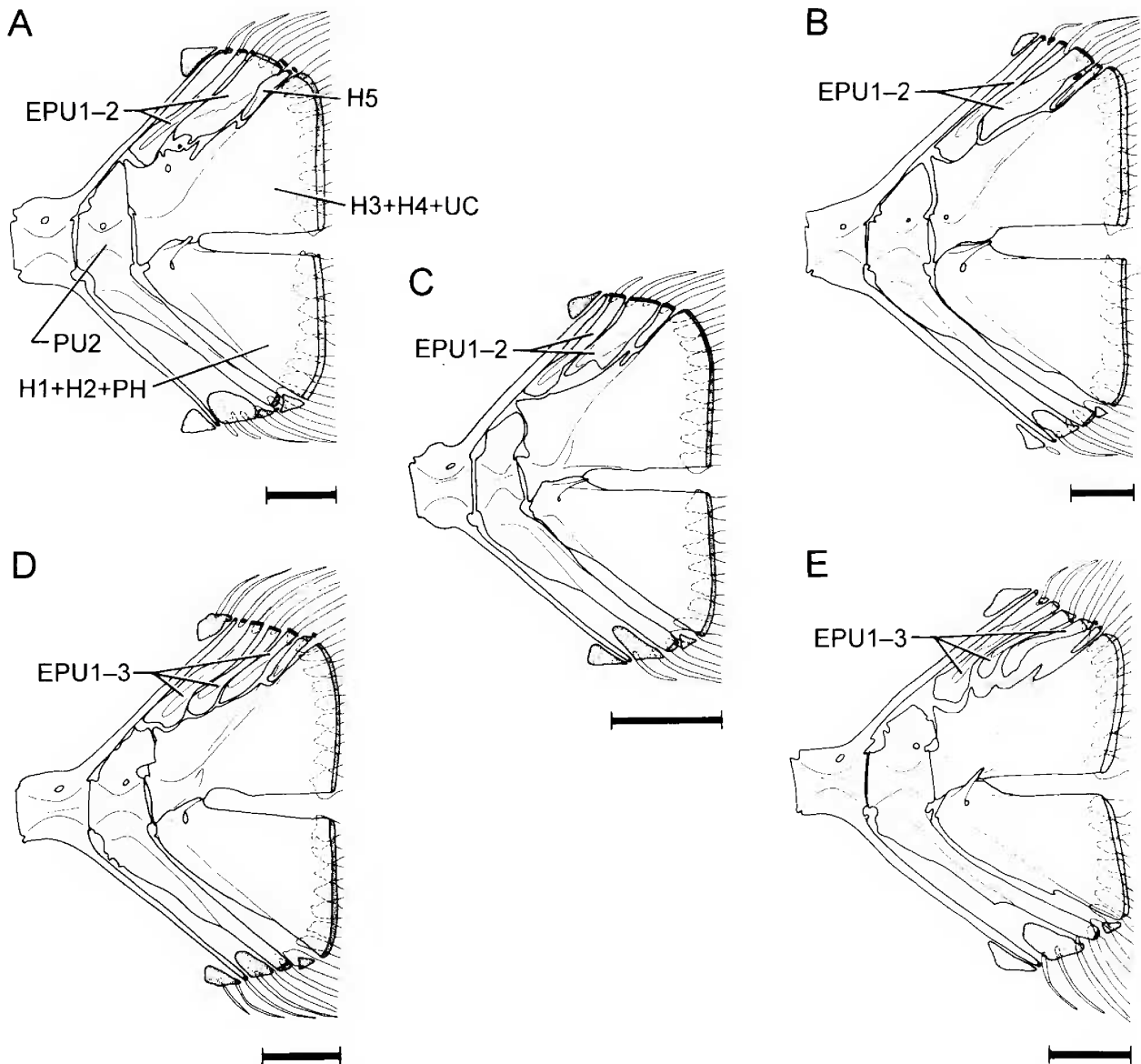


Figure 14. Caudal skeletons of selected pseudoplesiopine species in left lateral view: A, *Lubbockichthys* sp. 1, AMS I.25107-067, 47.3 mm SL; B, *Pseudoplesiops typus*, AMS I.19442-013, 50.6 mm SL; C, *Amsichthys knighti*, AMS I.22612-034, 28.3 mm SL; D, *Chlidichthys johnvoelckeri*, CAS 35451, 37.9 mm SL; E, *Pectinochromis lubbocki*, BPBM 28119, 35.5 mm SL (paratype). Cartilage shown in dense stipple; overlapping portions of fin-ray bases shown in broken lines. Abbreviations: EPU1-3, epurals 1-3; H1+H2+PH, fused hypurals 1 and 2 and parhypural; H3+H4+UC, fused hypurals 3 and 4 and compound urostyle complex; H5, hypural 5; PU2, preural centrum 2. Scale bars = 1 mm.

of *Chlidichthys* and *Pectinochromis* (see Character 12 above). The outgroup taxa have the upper two preopercular pores relatively close together, and most have relatively high numbers of preopercular pores: 12-16 for anisochromines; 10-19 for *Assiculoides*; and 9-18 for *Assiculus*. Congrogadines usually have only six or seven preopercular pores (nine in the relatively derived species *Halidesmus polypterus*), but the upper two pores are not widely separated. Therefore, the condition shown in *Chlidichthys* and *Pectinochromis* is considered apomorphic within the Pseudoplesiopinae.

Character 29. Ten precaudal vertebrae. Lubbockichthys,

Amsichthys and almost all *Pseudoplesiops* species have more than ten precaudal vertebrae (Table 2; state 0), as do most of the immediate outgroup taxa: 12-19 in congrogadines; 11-12 in *Assiculoides*; and 11 in *Assiculus*. *Chlidichthys* and *Pectinochromis* are unusual among pseudoplesiopines in having ten precaudal vertebrae (Table 2; state 1). Anisochromines, one relatively derived *Pseudoplesiops* species and most pseudochromines (the only exceptions are *Assiculoides*, *Assiculus* and *Labracinus*) also have ten precaudal vertebrae. However, parsimony dictates that the presence of ten precaudal vertebrae is apomorphic within the Pseudoplesiopinae.

Character 30. Eye large. Most pseudoplesiopines have relatively small eyes: 8.5–10.6% SL in *Chlidichthys*, 7.9–11.7% SL in *Lubbockichthys*, and 8.2–11.0% SL in *Pseudoplesiops* (state 0). *Pectinochromis* and *Amsichthys* are distinctive in having relatively large eyes, 10.5–11.9 and 9.9–12.5% SL, respectively (state 1); overlap with smaller-eyed taxa can largely be attributed to ontogenetic variation (smaller specimens have proportionally larger eyes). Outgroup taxa have relatively small to moderate eyes; the condition shown by *Amsichthys* and *Pectinochromis* is therefore considered apomorphic.

Character 31. Dorsal-fin-ray branching. *Pseudoplesiops*, *Amsichthys* and *Chlidichthys* have mostly simple (unbranched) segmented dorsal-fin rays (state 0). *Lubbockichthys* and *Pectinochromis* have mostly branched segmented dorsal-fin rays (state 1). The first outgroup has mostly branched rays in this fin, whereas the second and third outgroups have mostly simple rays in the dorsal fin. Polarisation of this character is therefore equivocal within the Pseudoplesiopinae.

Character 32. Segmented anal-fin rays mostly simple. *Lubbockichthys* and *Pectinochromis* have mostly branched segmented anal-fin rays, as do the outgroup taxa (state 0). Conversely, the remaining pseudoplesiopine genera have mostly simple segmented anal-fin rays (state 1). The latter condition is therefore apomorphic within the subfamily.

Results of Parsimony Analysis. Phylogenetic analysis of the 32 characters (Table 1) resulted in the single tree shown in Fig. 15: tree length = 36; consistency index = 0.91; retention index = 0.76. [A second analysis was also performed using only characters 20–32, with character 26 recoded as “1” for *Chlidichthys*. In so doing, untested characters (synapomorphies of the Pseudoplesiopinae, and unique, unequivocal generic autapomorphies) were excluded. The analysis yielded the same tree, with the following statistics: tree length = 16; consistency index = 0.81; retention index = 0.76.]

Characters supporting monophyly of the Pseudoplesiopinae and its genera are discussed above in the diagnoses for the respective taxa.

Three synapomorphies support monophyly of a clade consisting of *Chlidichthys*, *Amsichthys*, *Pectinochromis* and *Pseudoplesiops*: segmented pelvic-fin rays all unbranched (character 20); posterior otic pores absent (character 21); and anterior temporal pores absent (character 22). One additional character, posterior interorbital pores (character 23), either supports monophyly of the clade (state 1), or is an autapomorphy of *Lubbockichthys* (state 0); the equivocal nature results from the presence of both states in the outgroup taxa (state 0 in the first outgroup, state 1 in the second and third outgroups), and the basal position of *Lubbockichthys* within the Pseudoplesiopinae. Similarly, mostly unbranched anal-fin rays (character 32) and mostly unbranched dorsal-fin rays (character 31), provide equivocal support for the clade consisting of *Chlidichthys*, *Amsichthys*, *Pectinochromis* and *Pseudoplesiops* (see below).

A single synapomorphy supports a sister-group relationship between *Amsichthys* and *Pseudoplesiops*: third supraneural bone well developed (character 24). However,

as this character varies within *Pseudoplesiops*, and is intraspecifically variable in *C. abruptus*, support for this relationship is weak. The distribution of one other character, segmented anal-fin rays mostly simple (character 32), is equivocal; it either supports monophyly of *Amsichthys* + *Pseudoplesiops* (and occurs homoplastically in *Chlidichthys*), or diagnoses the more general clade that also includes *Chlidichthys* and *Pectinochromis*, with autapomorphic reversal in the latter genus. Mostly unbranched dorsal-fin rays (character 31) provides similar equivocal support for a sister relationship between *Amsichthys* and *Pseudoplesiops* (see below).

Five synapomorphies support a sister-group relationship between the Indian Ocean taxa *Chlidichthys* and *Pectinochromis*: three epurals (character 25); infraorbital 2 reduced or absent (character 26); laterosensory-canal-bearing bones weakly developed (character 27); second preopercular pores absent (character 28); and ten precaudal vertebrae (character 29).

Character 30—eyes large—is most parsimoniously interpreted as independently derived autapomorphies of *Pectinochromis* and *Amsichthys*.

The presence of mostly unbranched segmented dorsal-fin rays (character 31) has been cited as an autapomorphy of the Pseudoplesiopinae (Smith, 1954; Springer *et al.*,

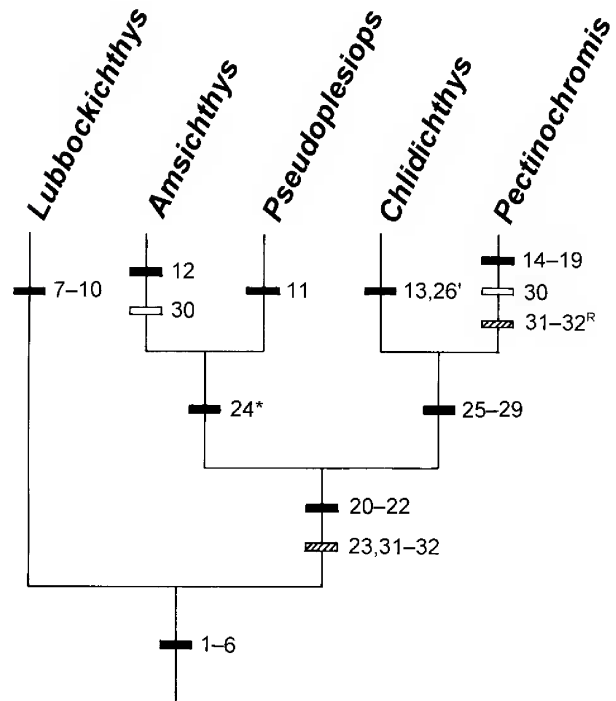


Figure 15. Cladogram of relationships between pseudoplesiopine genera generated from matrix in Table 1. Numbers indicate characters that support relationships (see text for details): solid bars indicate uncontradicted synapomorphies; open bars indicate homoplastic characters with unequivocal optimisations; hatched bars indicate homoplastic characters with equivocal distributions (see text for alternative optimisations); R indicates characters that reverse; * indicates characters that reverse within some derived (non-basal) species in terminal taxa; ' indicates derived state of multistate character.

Table 2. Comparison of selected characters of pseudoplesiopine genera. * Anterior extent of predorsal scalation is expressed in terms of proximity of anterior edge of first scale to either interorbital or supratemporal laterosensory commissure.

genus	dorsal-fin rays	anal-fin rays	pectoral-fin rays	pelvic-fin rays	total caudal-fin rays	vertebrae	anterior extent of predorsal scalation*	scales in lateral series
<i>Amsichthys</i>	I,23–24	I–II,13–15	16–18	I,4	24–25	11 + 18	interorbital	30–33
<i>Chlidichthys</i>	II,21–24	II–III,12–15	16–19	I,4	25–29	10 + 17–19	supratemporal to interorbital	37–52
<i>Lubbockichthys</i>	II,24–26	II,14–16	16–19	I,4	24–27	12–14 + 17–19 = 30–32	supratemporal	51–66
<i>Pectinochromis</i>	II,22–23	II,12–13	16–17	I,4	22–24	10 + 16–17	interorbital	35–39
<i>Pseudoplesiops</i>	I–II,22–29	I–III,13–18	15–18	I,3–4	23–26	10–14 + 17–21 = 28–33	supratemporal to interorbital	26–42

1977; Godkin & Winterbottom, 1985). However, the present analysis reveals that this character is homoplastic, with both character states occurring within the subfamily and its immediate outgroups. There are three equally parsimonious optimisations of the character, none of which provides support for monophyly of the Pseudoplesiopinae: (1) rays mostly branched (state 1) a synapomorphy of the Anisochrominae + Congrogadinae + Pseudoplesiopinae clade, with reversal to mostly unbranched rays (state 0) in the clade consisting of *Amsichthys*, *Chlidichthys*, *Pectinochromis* and *Pseudoplesiops*, and autapomorphic acquisition of mostly branched rays in *Pectinochromis* (accelerated transformation optimisation); (2) independent acquisition of branched rays in Anisochrominae + Congrogadinae, *Lubbockichthys* and *Pectinochromis* (delayed transformation optimisation); and (3) mostly branched rays a synapomorphy of the Anisochrominae + Congrogadinae + Pseudoplesiopinae clade, with independent reversal to mostly unbranched rays in *Chlidichthys* and in the clade consisting of *Pseudoplesiops* and *Amsichthys*.

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